

ECOLOGICAL AND SENSORY ASPECTS OF PREY CAPTURE BY
THE WHIRLIGIG BEETLE *DINEUTES DISCOLOR*
(COLEOPTERA: GYRINIDAE)

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Abstract.—Whirligig beetles prey on a variety of small soft-bodied invertebrates that enter their surface film habitat from above or below. They also act as scavengers on dead floating invertebrates. Deficits in prey capture ability were produced by experimental deprivation of visual, tactile, or surface vibration cues. Visual deprivation and deprivation of surface vibration cues produced statistically equivalent deficits in whirligig predatory behavior. When tactile and surface vibration cues were both unavailable to the beetles, the deficits in their predatory behavior were more pronounced. These sensory systems are similar to those of Hemipteran predators that live in the surface film.

The way a predator locates its prey is determined by the predator's environment, its endowment of sensory structures, and the nature of its prey. For whirligig beetles, all three of these factors are unusual. These beetles live and feed on the surface film of bodies of fresh water, and gyrid sensory structures are highly specialized for this environment. Their separate pairs of compound eyes above and below the water (Fig. 1) possess different spectral sensitivities suited to their respective surroundings (Bennett, 1967; Carthy and Goodman, 1964; Pappas, 1974). The Johnston's organs of their antennae, running between pedicel and flagellum (Fig. 2), are modified into extremely sensitive surface vibration detectors (Eggers, 1926; Wilde, 1941) which can sense vibrations with an amplitude as small as a few microns (Rudolph, 1967). Gyrinids potentially have available to them prey that enter the surface film from the air, from underwater or that live in the surface film itself.

I have examined the predatory activities of the river dwelling species *Dineutes discolor*, working in both the field and the laboratory to determine the natural diet of the beetles and what sensory systems were involved in their prey capture behavior. I investigated for the use of visual, tactile, and surface vibration cues in gyrid predation, all three of which are used by surface film dwelling water striders or backswimmers (Murphey, 1971a, 1971b, 1973; Murphey and Mendenhall, 1973). Prey animals in the surface



Fig. 1. Front and side views of the head region of *Dineutes discolor*, showing the separate dorsal and ventral pairs of compound eyes.

film are known to generate distinctive surface vibrations by their movements (Lang, 1980) which constitute an unusual stimulus available to any predator in contact with the water's surface.

MATERIALS AND METHODS

I studied an aggregation of whirligigs located on the Wisconsin River near Arena (Iowa Co.). Field observations were carried out with binoculars; for laboratory study beetles were removed from the river and maintained on a diet of live flightless *Drosophila*. Of the approximately 600 beetles examined for identification during the summers of 1976 and 1977, all but two were *Dineutes discolor*. This group composition differs from the multispecies rafts found in a lake habitat by Heinrich and Vogt (1980).

Beetles observed feeding in the laboratory belonged to one of four treatment groups. The first was normal beetles, which underwent no manipulation of their sensory structures. The second group was temporarily visually deprived, by exposing them to light from a Westinghouse DXC 500-W Photoflood from a distance of 30 cm. The exposure was carried out in a special reflector-lined aquarium freshly filled with cool water, so that the beetles were protected from elevated temperatures (they always submerged when the light was turned on). Once bright-light adapted, this group was observed feeding under a dim red light for 9 min. The combination of bright-light adaptation, a short observation period, and the insensitivity of the gyrinid eye to red light (Bennett, 1967; Carthy and Goodman, 1964) produced the visual deprivation. The third group was deprived of surface vibration cues by having their antennal flagellae removed. The Johnston's organ stretched between pedicel and flagellum (Fig. 2) depends upon relative motions of these two parts to detect surface vibrations (Eggers, 1926; Wilde, 1941). The fourth group was deprived of sensory cues by removal of both their antennal

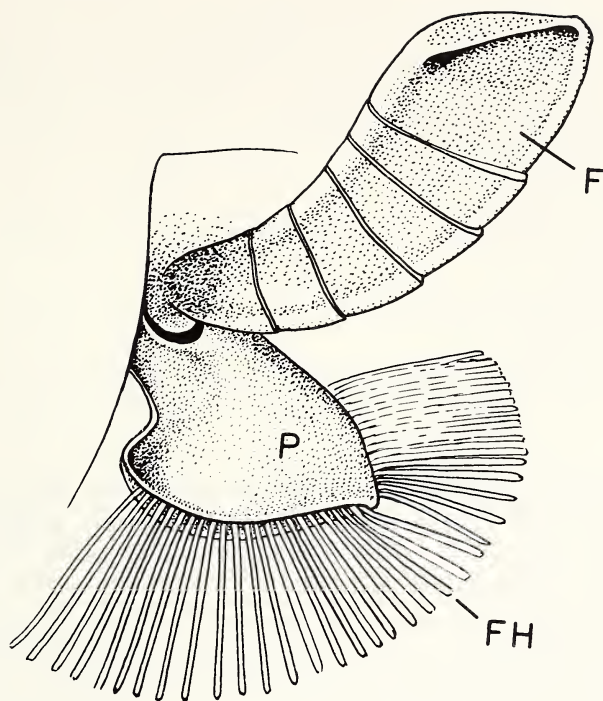


Fig. 2. The antenna of *Dineutes discolor*. Labelled parts are flagellum (F), pedicel (P) and socketed flotation hairs of the pedicel (FH).

pedicels and flagellae. Inspection with a scanning electron microscope revealed that the row of hairs on the pedicel have the typical individually socketed structure of mechanoreceptors, and so beetles with both pedicels and flagellae removed were deprived of tactile cues from these hairs as well as surface vibration cues. (Unfortunately it was impossible to eliminate the hairs on the pedicel and leave the surface vibration detectors intact, as these hairs supply the buoyancy that keeps the antennae afloat, and removing them causes unpredictable changes of the height at which the antennal pedicels are floating.)

Beetles were observed in the laboratory one at a time, feeding on live flightless *Drosophila* in a $122 \times 122 \times 30$ cm tank that rested on inflated inner tubes to insulate it from extraneous environmental vibrations. Approximately 150 prey captures were recorded for each of the four treatment groups, with ten to twenty beetles comprising each group. Three or four days of food deprivation before observation periods was adequate to ensure hungry but otherwise healthy beetles.

Table 1. Objects close circled by *D. discolor* under natural conditions.

Objects close-circled	Consumed	Not consumed
Live invertebrates less than 3 mm long (gnats and collembolans)	4	3
Live mosquito larvae	3	88
Live flies, 3–5 mm long	2	—
Live flies, 5–10 mm long	1	1
Live coccinellid beetles	—	3
Dead spiders	18	—
Dead unidentified invertebrates	5	12
Duckweed plants	—	33
Unidentified objects	46	1,103

In both laboratory and field, *D. discolor* performs a stereotypic predatory sequence I call a close circle. The beetle approaches with its head directed toward its prey. Keeping its head very close to the prey the beetle circles around the prey. The raptorial forelegs of the whirligig, normally held in grooves under its body, reach out toward the prey during this circle. In the field, one, occasionally two, or rarely more, close circles were performed about prey animals before they were captured and consumed. For the laboratory data I compared the number of close circles required for prey capture as a measure of how the various sensory deprivations affected predatory ability.

RESULTS

A total of 1,322 close circles of objects in the surface film was recorded during the course of my field observations (Table 1). Identification of objects being close circled was often difficult due to their small size, as the categories in the table attest. Prey were only scored as "live" if I saw them move independently before being close circled by a gyrid.

All of *D. discolor's* prey were soft-bodied invertebrates. They entered the surface film both from above (gnats, collembolans, flies, etc.) and below (mosquito larvae). Although small pieces of vegetation were close circled, I never observed the beetles eating any plant material. Beetles occasionally dove below the surface, but even when they were surrounded by animals they would have attacked at the surface film (mosquito larvae), I never saw a submerged gyrid attack a prey animal.

In the laboratory, sensory deprivation in visual, surface vibration, and tactile stimuli all resulted in more close circles being required for prey capture. Figure 3 shows these data displayed as the cumulative probability of prey capture vs. the number of close circles performed, which is a form of

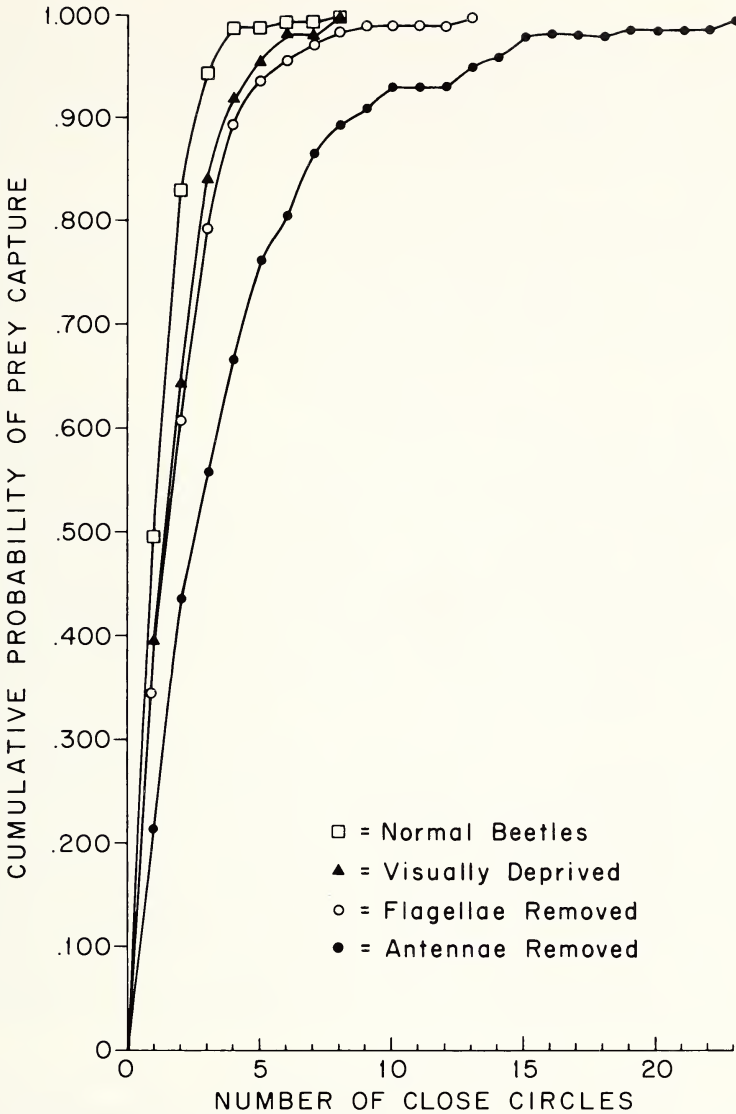


Fig. 3. The cumulative probabilities of prey capture by four experimental groups of *Dineutes discolor* fed live flightless *Drosophila* in the lab. The total number of prey captured is 150 ± 5 for each of the groups of beetles.

data organization amenable to analysis using the Kolmogorov-Smirnov test (Siegel, 1956). Each of the four groups of beetles includes data for 150 ± 5 prey captures.

Both visually deprived beetles and those deprived of their flagellae re-

quired more close circles than normal beetles to capture prey, with significance levels of 0.025 and 0.001 respectively. The visually deprived beetles and those deprived of surface vibration cues by flagellar ablation were statistically indistinguishable from one another in their number of close circles per prey capture, which can be seen by the virtual overlap of these two lines in Figure 3.

Beetles deprived of both surface vibration cues and tactile cues by having their antennae removed required even more close circles to capture prey, differing from all three previous groups at the 0.001 significance level. Presumably this deficit reflects an additional sensory deprivation due to the loss of mechanoreceptive hairs on their antennal pedicels.

DISCUSSION

Whirligig beetles capture and consume prey that enters the surface film from below and above, thereby taking advantage of aquatic insects that need to reach the surface for air, as well as flying or terrestrial invertebrates that may be blown down onto the water or landed in order to lay eggs. My limited ability to clearly distinguish small invertebrates and their movements from several meters distance undoubtedly skews Table 1 towards larger prey items and towards dead food materials more than is the actual case. Nonetheless, *D. discolor* clearly acts as both a predator and as a scavenger, and seems to feed on rather soft-bodied forms.

Virtually all of the live prey of *D. discolor* listed in Table I are very ephemeral objects from a whirligig's viewpoint. When approached by a predator in the surface film, mosquito larvae submerge, collembolans jump, gnats take off from the water's surface, etc. If a gyrenid is to successfully capture any prey, its predatory sequence must be as rapid as possible. The fewer number of close circles a gyrenid performs before prey capture, the more prey it will probably consume. This argument may also obtain for the dead invertebrates scavenged by the beetles. Not only do *D. discolor* live in moving water, but they also feed in aggregations and a dead invertebrate not captured immediately is apt to be swept downstream or consumed by a conspecific.

Previous studies have shown that backswimmers and water striders are capable of utilizing a variety of cues in locating and capturing prey, including visual, tactile and surface vibration cues (Murphey, 1971a, 1971b, 1973; Murphey and Mendenhall, 1973). Potential prey insects in the surface film generate distinctive vibration spectra (Lang, 1980) and the processes of surface vibration orientation are beginning to be unravelled (Lang, 1980; Reinig and Uhlemann, 1973; Weise, 1974).

D. discolor appears to use visual, tactile, and surface vibration cues in prey capture, as indicated by the increased number of close circles required in my laboratory groups. An alternative hypothesis for these deficits that must

be considered is that the beetles were physically damaged in a more general sense by their laboratory treatments, but I do not believe this to be the case. Normal beetles in Figure 3 show probabilities of prey capture with one and two close circles, respectively, that correspond to 77 and 129 out of 155 total prey captured. The normal laboratory animals were therefore capturing prey with one or two close circles, much as beetles do in nature. The visually deprived beetles were exposed only to bright light and my apparatus ensured that they were not subjected to elevated temperatures, and they show deficits in capture behavior statistically indistinguishable from those of the beetles with their antennal flagellae removed. Experimental beetles who were operated on were as vigorous as normal animals, and did not display an increased mortality. Ideally I would have performed sham operations, but there is no obvious way to do so when the procedure involves an ablation rather than an incision.

Congeneric whirligigs such as *Dineutes hornii* are largely quiescent during the day and forage at night (Heinrich and Vogt, 1980). This nocturnal feeding may rely upon different sensory modalities than the diurnal predation by *D. discolor*. Whether whirligigs forage at night or during the day appears to depend on the motion of the water in which they live; those that live in a current must climb out of the water onto emergent vegetation at night in order to avoid being swept downstream while unable to use visual cues to maintain their position relative to the shore (Brown and Hatch, 1929; Folkerts and Donovan, 1973).

The wave patterns produced by swimming gyrids have been well described by Tucker (1969), and the possibility of these waves reflecting off prey in a surface film borne echolocation system has seemed a natural possibility. However, the wavelengths of the waves produced by swimming gyrids are very large compared to the portions of the natural prey items in contact with the surface film (siphons for mosquito larvae, legs for gnats, etc.) and so efficient wave reflection for echolocation seems unlikely. It is more probable that any echolocation used by gyrids involves locating larger objects in the surface film, like rocks, conspecifics, etc.

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